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Understanding the impact of invasive crayfish

Francesca Gherardi

INTRODUCTION

In a rather provocative article, Parker *et al.* (1999) claimed that, up to now, little scientific attention had been placed on developing either theoretical or operational generalizations about the impact of invasive species. Specifically, the authors lamented the lack of a general framework in which to discuss ‘the impact is, or how we decide that the non-indigenous species exceeds that of another, or how we decide that the impact of a particular species is greater in one place than in another’ (Parker *et al.* 1999, p. 4). Today, this scenario has to have changed for several freshwater non-indigenous species (NIS), e.g. the zebra mussel *Dreissena polymorpha* (Pallas) (e.g. Karatayev *et al.* 2002, Ricciardi 2003), but it has remained practically unaltered for other widely distributed bioinvaders that have, however, attracted much scientific attention in the latest years, such as freshwater crayfish.

Crayfish are the largest and amongst the longest lived invertebrate organisms in temperate freshwater environments, and often exist at high densities. These species are keystone consumers (Nyström *et al.* 1996), feeding on both macroinvertebrates, detritus, macrophytes, and algae in lotic and lentic water bodies (Whitledge and Rabeni 1997). They also constitute the main prey of several vertebrate species, including otter (Slater and Rayner 1993), fish (e.g. Blake 1995), and birds (Rodríguez *et al.* 2005). Because of their capability to integrate into the food web at many levels and to persist on the substantial energy reserves in the detrital pool, crayfish are good candidates for invading aquatic systems (Gherardi and Light 1996).

the continents. Over 600 species have been described worldwide (Cain 2002), the majority occurring in North and Central America (75% of the total). About 100 indigenous species live in the southern hemisphere, 1 in Europe, four in Asia, and none in continental Africa and in Antarctica (Cain 1988, Fitzpatrick 1995, Taylor *et al.* 1996, Taylor 2002). We know today that much of their present distribution is due to human intervention, even for the most celebrated “indigenous” species. For instance, as reported by Linnaeus (1746, p. 358) and confirmed by Pontoppidan (1775, p. 175), the noble crayfish *Astacus astacus* (Linnaeus) seems to have been imported into Sweden from the Netherlands by John III (King of Sweden since 1568) and later into Finland (Westman 1991). Similarly, the white-clawed crayfish *Austropotamobius pallipes* (Lereboullet) has been introduced into Ireland by monastic orders from France in the 13th century, as suggested by Reynolds (1997). Genetic evidence for this hypothesis has recently been obtained by Gouin *et al.* (2003).

In the last few decades, as a result of the exponential growth in the volume and complexity of the international trade, the world distribution of crayfish has dramatically changed (e.g. Pérez *et al.* 1997) mostly due to transcontinental interstate translocations of a still relatively small proportion of crayfish species (hereafter referred to as NICS, i.e. non-indigenous crayfish species) – 20 according to Hobbs *et al.* (1989), but increasing all the time. Human-mediated translocations have been often accidental (in ballast, via canals, by escapes from holding facilities) but the introduction of some crayfish species was deliberate (for aquaculture and stocking, for food, as aquarium pets, as live bait, as a snail and weed control; see Lodge *et al.* 2000, Chapter 2). In Africa, the introduction of North American and Australian species from the 1970s onwards (Arrignon *et al.* 1990) was aimed to broaden the range of commercial fisheries in lakes and dams (Mikkola 1996) and to control freshwater snails that carry human schistosomiasis (Hofkin *et al.* 1991, Chapter 4). Indeed, crayfish introductions were motivated by our desire to eat them (Hobbs 1999a) that in its turn generates economic interests. Some species are highly valued as food, and in countries like Scandinavia and Louisiana fishing on them has become a cultural icon. As a consequence, for instance in Europe wild stocks are managed, leading to annual catches of more than 4,000 tonnes and some species are cultivated with a total production of about 150,000 tonnes (Ackefors 1999).

Hence, crayfish introductions have certainly provided economic benefits to several countries, because of (1) restoring the productivity of indigenous stocks (e.g. in Sweden), (2) compensating for their lack (e.g. in Spain), (3) developing extensive or semiintensive cultivation systems (e.g. in the People's Republic of China) (Ackefors 1999). However, once introduced for stocking in aquaculture and kept in outdoor ponds, crayfish of several species are inevitably escape (Hobbs *et al.* 1989) and a proportion of them is able to establish self-sustaining populations in the colonized habitats. The inva-

point of introduction, others spread widely, becoming invasive (Kolar and Lodge 2001). Compared to other aquatic species, the spread of this taxon is favored by the ability of some species to stay for relatively long periods in water and to travel long distances, sometimes overland [e.g. *Procambarus* (Girard), Gherardi and Barbaresi 2000]. Contradicting the predictions made by the tens rule (Williamson 1996), the majority of the naturalized populations have the potential to become noxious. For instance, of the eight NICS imported to Britain since 1970 five have been found in the wild and four of these have become established, three being now officially classified as pests (Hobbs 1999b). Today, the list of species that are causing concern in the introduced areas includes *Pacifastacus leniusculus* (Dana) in California (USA), Europe, and Japan, *Orconectes limosus* (Rafinesque) in Europe, *Orconectes rusticus* (Girard) in North America, *P. clarkii* in Africa, California, Europe, and Japan, *Ampelisca leptodactylus* Eschscholtz in some European countries, and *Cherax destructor* Clark in Africa and Australia (Holdich 1999a). Other species, like *Cherax quadricarinatus* (von Martens) in Ecuador, are expected to lead problems in the future (Romero 1997).

Concerns relate to the modifications that NICS may induce in the structure of freshwater food webs (e.g. Lodge *et al.* 1998) and the economic damage they may inflict through, for instance, reduced recruitment of commercially valuable fish stocks (Nyström 1999). In the short term, they may decrease the biomass and species richness of macroinvertebrates, macrophytes, and periphyton (e.g. Lodge and Lorman 1987) and, in the long term, they may contribute to the decline of several invertebrate taxa, including indigenous crayfish species, amphibians, and fish (e.g. Guan and Wiles 1997, Chapter 29). Once added to the existing system, NICS have the potential to impose “considerable environmental stress” and, in most instances, they may induce “irreparable shifts in species diversity” (Hobbs *et al.* 1989, p. 309).

In this chapter, the literature focusing on the multiform “environmental stress” that NICS have been found to pose to the colonized areas around the world will be reviewed, as well as the “shifts in species diversity” that they have caused. In addition, information about their effects upon human economic health will be discussed. By identifying several gaps in the existing literature, I will suggest the directions that research should take to extend and strengthen the current knowledge of the impact of NICS and to help prioritize interventions in freshwater systems.

THE LITERATURE ON THE IMPACT OF NICS

Since the 1980s, the effects exerted by NICS on the environment, indigenous species, national economies, and human health have been abundantly publicized (e.g. Holdich 1988, 1999a, Hobbs *et al.* 1989, Gherardi and H

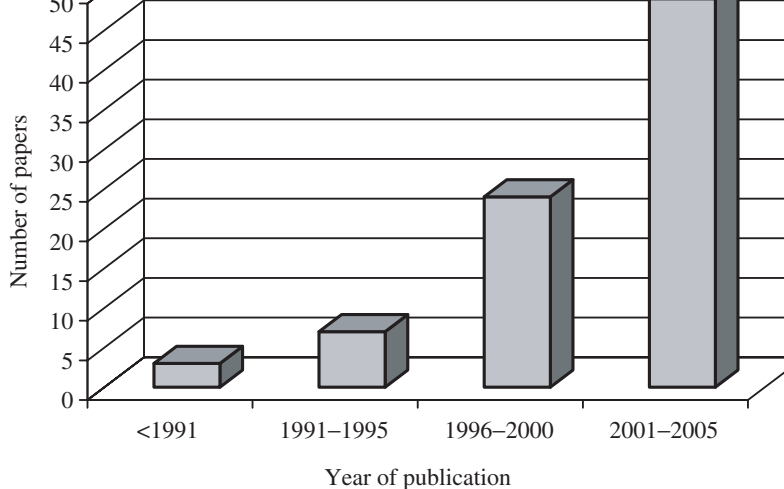


Fig. 1 The rise in the number of publications that described the impact of non-indigenous crayfish species (NICS). Papers (reaching a total of 103) were identified by searching keywords from Biosis (1967–February 2006), ASFA (1960–March 2006), and Biological Record (1978–March 2006). Only papers reporting quantitative data published before 2006 (83) are included here.

1999, Lodge *et al.* 2000). The International Association of Astacology (IAA) contributed in heightening awareness about the negative impact of NICS by adopting a resolution in 1987 (VII Symposium Lausanne, Switzerland) in which governments were recommended to “find the means to stop the importation of living crayfish into their countries for any purpose... except for governmentally approved research, restockings or introductions”. This resolution was subsequently renewed (in: 1997, Florence, Italy; 1998, Amsterdam, Holland and Augsburg, Germany, and 2002, Querétaro, Mexico).

The consequent surge of interest in NICS encouraged more proactive research and led, since 1987, to a sharp increase, mostly in Europe, in the number of publications, that included 18 reviews (e.g. Holdich 1999a, Lodge *et al.* 1999, Nyström 2002, Westman 2002, Geiger *et al.* 2005), focused on describing the impact of some NICS (Fig. 1), particularly *P. clarkii* and *P. leniusculus* (Forsgren 1999). The studies that have attempted to quantify impacts have often done so using an experimental approach (reviewed in Chapter 30). However, short-term researches largely prevailed: only 12% of the 85 quantitative studies analyzed monitored the effects of NICS on a system for more than 1 year. Some of these studies adopted classical *in situ* enclosure/exclosure experiments to analyze the effects of NICS on the abundance of several components

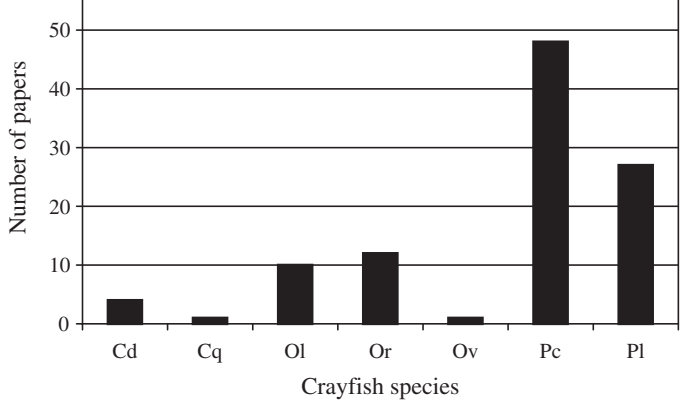


Fig. 2 The number of publications describing the impact of NICS (103, see Table 1) is distributed among crayfish species. Cd = *Cherax destructor*; Cq = *C. quadricarinatus*; Ol = *Orconectes limosus*; Or = *O. rusticus*; Ov = *O. virilis*; Pc = *Procambarus*; Pl = *Pacifastacus leniusculus*.

resident community. Lodge *et al.* (1994) pioneered this experimental approach by revealing the control of *O. rusticus* on the trophic interactions existing in the littoral zone of some North American lakes.

Several other studies applied a correlative approach by comparing NICS with indigenous crayfish species for growth rate, densities, vulnerability to predation, predatory ability, and behavioral dominance over food and shelter. On the other hand, the impact exerted on macrophytes and benthic invertebrate abundance has been elegantly compared between invasive and indigenous species through a combination of field and laboratory experiments (e.g. Olsen *et al.* 1999). In the other, to test the ability of several NICS to outcompete indigenous crayfish, experiments were mostly run in the laboratory (e.g. Söderbäck 1991, Hultine *et al.* 1995, Vorburger and Ribí 1999, Gherardi and Cioni 2004).

Ideally, much knowledge of the effects of NICS on the community should derive from the comparison (1) of one site before and after their invasion and (2) of different sites, with and without an invader present, at the same time. Unfortunately, only a small minority of studies (e.g. Rodríguez *et al.* 2004, McCarthy *et al.* 2006) adopted this comparative approach, in large part because the interest in an invasive species most often arises after it has spread extensively and only when it has already had an impact. An obvious drawback of these studies is that results may be confounded by temporal or spatial variations in the environment such as pollution, harvesting, or climate change. Studies should therefore be accompanied by a thorough documentation of any contemporary modifications in the habitat.

estimate of the relative impact of a species between its native and introduced habitats. Indeed, this comparison would be critical to assess the varying strength of an invasive species. Evolutionary history in fact plays a major role in this process and invasive species may display greater impacts in systems with native co-evolved predators, parasites, and prey (see e.g. the “enemy release” hypothesis, Torchin *et al.* 2003). This is well illustrated by the impact of the North American *P. leniusculus* in the UK (Holdich *et al.* 2004).

THE FIVE LEVELS OF ECOLOGICAL IMPACTS

According to Parker *et al.* (1999), the impact of an invader can be measured at five levels of biological complexity: (1) effects on individuals (life history, morphology, behavior); (2) population dynamic effects (abundance, population growth, etc.); (3) genetic effects (including hybridization); (4) community effects (species richness, diversity, trophic structure); and (5) effects on ecosystem processes (nutrient availability, primary productivity, etc). An overview of the literature on NICS clearly shows that some of these effects are documented much more than others (Fig. 3). The most understudied impacts were genetic changes that, on the contrary, should require much more attention by invasion biologists. They may in fact give rise to new invasive forms, induce decline

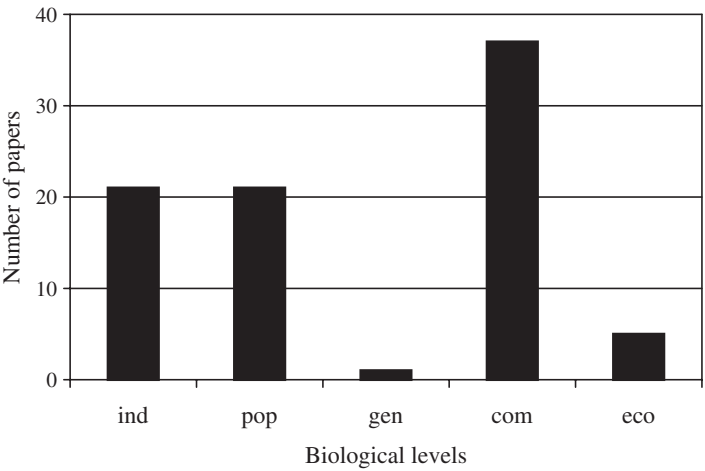


Fig. 3 The number of studies (85) reporting quantitative data on the impact of invasive species at five different biological levels: individual (ind), population (pop), genetic (gen), community (com), and ecosystem function (eco). Single studies that reported impacts at more than one level were classified on the basis of the most prominent one.

to long-term evolutionary shifts (Cox 2004).

The best examples of studies, classified at the biological level, which quantified the impact of NICS, are reviewed below.

Effects on individuals and populations

The development of predator-prey or competitive interactions is expected to induce changes in the life history, morphology, and behavior of the interacting species. These changes are obviously adaptive as they should reduce the risk for the “weaker” species to be preyed upon or to be outcompeted by the “stronger” species (e.g. Lima 1998). When, on the contrary, no adaptation appears, the changes undergone do not suffice to develop a balance between the prey and the new predator or between competitors, the abundance, population dynamics, and distribution of the “weaker” species – usually the indigenous species – may be strongly affected. The most extreme effect at the population level is extinction, either at the local or even at the global level.

Several studies have focused on an NICS acting as a predator upon a native species, either invertebrate or vertebrate. Most often they showed lethal or sublethal effects. For instance, *P. leniusculus* easily consumes *Lymnaea stagnalis* (Linnaeus) and induces tail-cuts to *Rana temporaria* (Linnaeus) tadpoles (Nyström 2001); *P. clarkii* (1) is able to prey upon the embryos and free swimming larvae of up to 13 amphibian species (Cruz and Rebelo 2005); (2) takes a significantly shorter time than the indigenous *A. pallipes* to capture *Triturus cristatus* (Linnaeus) larvae and *Rana esculenta* Linnaeus tadpoles (Renai and Ghisler 2004); or (3) is not deterred by toxins contained in Californian newt [*Taricha torosa* (Rathke)] eggs (Gamradt and Kats 1996).

Obviously, lethal or sublethal effects exerted by NICS are mostly due to the relatively short coevolutionary history between them and the naïve prey species. This does not allow the latter to develop efficient antipredator behaviors, morphological structures, or chemical repellents. The absence of these mechanisms has been evoked to explain, for instance, the sharp decline of the California quail recorded in three streams in the Santa Monica Mountains of southern California after about 10 years from the introduction of *P. clarkii* (Gamradt and Kats 1996).

However, historical coexistence in the area of origin seems not to be the only prerequisite for the exhibition of efficient antipredator behaviors: notwithstanding their common history in the area of origin, naturalized mosquitofish [*Gambusia holbrooki* (Girard)], once exposed to visual and chemical stimuli by *P. clarkii* in a confined environment in Portugal, did not decrease their activity and did not avoid spaces with high predation risks (Leite *et al.* 2005). Mosquitofish were therefore subject to a strong predation pressure by the NICS, as confirmed from the frequent occurrence of their remains in crayfish gut contents (Gutiérrez-Yurrita *et al.* 1998, Correia 2003).

cues released by injured conspecifics (alarm odors). For instance, when exposed to alarm odors, the snail *Physa gyrina* (Say) significantly increases its spatial refugia by moving to the waterline, floating at the surface, or crawling out of the water (McCarthy and Dickey 2002). These behaviors were independent of the predator's identity and therefore were exhibited in the presence of both the known *Orconectes juvenilis* (Hagen) and the unknown *P. clarkii*.

In only one case was it found that the prey, although naïve, had previously acquired the ability to recognize an NICS as a predator. An ecological experiment conducted in Pennsylvania (USA), revealed that the snail *P. gyrina* moved under cover in the presence of pumpkinseed sunfish but moved to the water surface in the presence of *O. rusticus*; the combined effects of fish and crayfish were intermediate to their individual effects (Turner *et al.* 2000). On the one hand, these results can explain why periphyton standing crop in covered habitats was the lowest in the fish treatment when covered habitat use by snails was the highest, and the highest in the control and in the crayfish treatment when covered habitat use by snails was the lowest. On the other hand, they show that the prey has learned some stimuli emitted by the NICS (possibly its odor) and behaves accordingly to avoid it. This is not the typical response shown by the snail to a generalized predator. On the contrary, the snail seems to be able to distinguish the specific identity of *O. rusticus* with respect to fish predators. The behavioral responses to predatory NICS by potential prey, leading, for instance, to changes in their microhabitat selection, diurnal activity or foraging patterns, have never been studied.

As regards to competitive interactions, few studies have analyzed the effects induced on non-crayfish species by resource competition with NICS. In a laboratory setting, Carpenter (2005) conducted density manipulation experiments to analyze the competition between *O. virilis*, established in the Colorado River basin, and two endemic fish species, the Gila chub, *Gila intermedia* (Girard), and the flannelmouth sucker, *Catostomus latipinnis* (Baird and Girard). The results showed that growth of flannelmouth suckers, but not of Gila chub, was affected by crayfish more than by intraspecific competition, leading to the conclusion that each case of competitive interaction should be taken as a separate case. At a population level, the ability of crayfish to outcompete other fish species, for instance by expelling individuals from their shelters and therefore by making them more vulnerable to piscivorous fish, may have detrimental effects. In six riffles of the River Great Ouse (England), the number of *P. leniusculus* and of the two dominant benthic fish, bullhead [*Cottus asotus* (Linnaeus)] and stone loach [*Noemacheilus barbatulus* (Linnaeus)], were inversely correlated (Guan and Wiles 1997; other examples in Chapter 2).

The most commonly documented impact of NICS on competitive interactions is the agonistic dominance they show over indigenous crayfish species (Chapter 31), with the only known exception of *Astacopsis franklinii* (Gray), endemic

destructor (Elvey *et al.* 1998), which exposed in the laboratory to an indigenous crayfish changed their posture and behavior, quickly assuming the role of subordinates [e.g. *Procambarus acutus acutus* (Girard) vs. *P. clarkii*, Gherardi and Daniels 2004]. When, however, stable dominance hierarchies between NICS and indigenous crayfish species cannot be formed, as observed in the case of *P. clarkii* and *A. pallipes* (Gherardi and Cioni 2004), the repetition of escape fights may lead to injuries usually suffered by the weaker indigenous crayfish, followed by its likely death. Indeed, NICS, e.g. *P. leniusculus*, may prey upon indigenous *A. pallipes* and *A. leptodactylus*, and predation may have contributed to the gradual decline of *A. pallipes*, at least in England (Holdich and Newbould 1995).

Dominance hierarchies usually translate into a differential capability to compete for resources, such as shelters. It is known that shelters act as a “priority resource bottleneck” in crayfish populations (Hobbs 1991) serving to minimize predation risks and in some species to attract mates (Gherardi 2002). The availability is usually limited so that an inferior ability to compete for them may lead to a higher susceptibility to predation in subordinate species, being therefore a major cause of their increased mortality (Gherardi and Cioni 2004). When tested in the laboratory, dominant NICS were most often found to competitively exclude subordinate indigenous crayfish from the offered shelter [in: *O. rusticus* vs. *Orconectes* species, Hill and Lodge 1999; *P. leniusculus* vs. *A. astacus*, Söderbäck 1991; and *P. leniusculus* vs. *Cambaroides japonicus* (De Haan), Usio *et al.* 2003; Nakata and Goshima 2003] also when NICS showed a low preference for the shelter in a noncompetitive context [*P. clarkii* vs. *A. pallipes*, Gherardi and Daniels 2004, and vs. *P. acutus acutus*, Gherardi and Daniels 2004; but not *P. leniusculus* vs. *Austropotamobius torrentium* (Schränk), Vorburger and Ribi 1999]. Although conducted in an artificial setting, the results of these experimental studies are both informative and predictive, being a reflection of the documented expansion of NICS. In fact, those crayfish species that were found to resist against other crayfish species are also dominant in interspecific contests staged in the laboratory (e.g. Capelli 1982, Söderbäck 1991, Hill and Lodge 1994).

Predation and competition, both acting at the individual level and contributing with the potential for reproductive interference (i.e. females or males of a species may choose mates of the other species; Söderbäck 1994), enhance the effects of habitat loss, overexploitation, and pollution in inducing a dramatic decline in crayfish biodiversity. Of the 67 threatened species in North America, 5% are subject to interference by NICS, 62% to habitat degradation or habitat loss, and 33% to pollution (Wilcove *et al.* 1998). NICS have already contributed to the global extinction of other crayfish species: *Pacifastacus nigrescens* (Stimpson), once common in the creeks of the San Francisco Bay area in northern California, is now extinct due to the combined pressures of urbanization, overexploitation, and introductions of NICS (Bouchard 1977). In the Shasta area, a similar process is ongoing. Shasta crayfish [*Pacifastacus fortis* (Faxon)]

having been displaced at several locations in its native watershed by *P. leniusculus* (Light *et al.* 1995). Subject to threats from NICS, the European indigenous species *A. astacus*, *A. pallipes*, and *A. torrentium* have been designated as vulnerable by Groombridge (1993) as protected in Appendix III of the Bern Convention. The European Habitat Directive (Directive 92/43/EEC) considers them as species whose exploitation and harvesting should be subject to control. *Austropotamobius pallipes* and *A. torrentium* are also listed in Appendix V, as species that require the setting up of special areas of conservation for their protection (Souty-Grosset *et al.* 2006).

Population effects on indigenous species may also be caused by indirect mechanisms, for instance through the transmission of pathogens and diseases. There is an extensive literature showing that North American crayfish species can carry a subclinical infection of the oomycete *Aphanomyces astaci* Schikore, the aetiological agent of the crayfish plague (e.g. Alderman and Polglase 1986, Diéguez-Urbeondo and Söderhäll 1993). This disease does not require direct contact in order to spread, as the spores can become attached to damp surfaces and be transported in this manner. So, crayfish plague has spread and is still spreading via the hundreds of thousands of crayfish trappers and their gear. A large number of European crayfish populations has been decimated by the plague since 1860, leading to reduced production of *A. astacus* and *A. leptodactylus* up to 90% particularly in Scandinavia, Germany, Spain, and Turkey. For example, in Sweden 90 tons were exported in 1908 (from a total catch of 100 tons), but export dropped to 30 tons by 1910 (Holdich 1999a). In Finland exports declined from 16 million *A. astacus* in 1890 to less than 2 million in 1910 (Westman 1991). When the plague spread to Turkey in the 1980s, the annual catch of *A. leptodactylus* plunged from 7,000 to 2,000 tons (Işık 1988). It declined even further in the early 1990s, reaching 200 tons in 1991, which virtually eliminated exports from Turkey to western Europe. However, since then there has been a steady increase in stocks (Harvey 2004). The impact of the crayfish plague is still high in Europe; to manage this, it has even been suggested that plague-resistant strains of native species should be created through genetic engineering (Westman 2002), which in their turn, might pose additional threats to the original biodiversity.

The large emphasis that researchers have given to *A. astaci* has created a bias. Edgerton *et al.* (2004) lamented, a kind of “inertia” in astacology, “which has curtailed researchers, state fish-disease diagnosticians, and resource managers from fully assessing and considering the existence of other serious pathogens of crayfish and the ensuing consequences for the native species” (p. 1). Indeed, notwithstanding that the range of crayfish diseases is repeatedly assumed to be much wider than previously thought (e.g. Vogt 1999), especially in North America, little attention has been given to commensal parasites other than *A. astaci*. It seems unlikely that these pathogen

may profoundly affect indigenous species. To make the picture worse, commensals or parasites of crayfish may affect other animals, humans included (helminth parasites of vertebrates; Hobbs *et al.* 1989; bacterial fish diseases; enteric redmouth, Dunlin *et al.* 1976; infectious pancreatic necrosis, F and Ahne 1988). As a consequence, there is an urgent need for research to address the issue of crayfish diseases from a broader perspective than has been done up to now.

Genetic effects

Invaders may exert indirect genetic impacts on indigenous species, resulting in altered patterns of natural selection or gene flow within indigenous populations. They may change selection regimes or, in a subtler way, disrupt gene flow, for instance, to their fragmenting populations of indigenous species and expose them to risky bottlenecks. Hybridization between an invader and an indigenous species is a direct effect that may have three possible consequences: (1) the creation of a new invasive genotype; (2) the production of sterile hybrids and the resulting waste of gametes and resource competition with indigenous species; and (3) the production of a hybrid swarm and widespread introgression leading to a virtual extinction of indigenous taxa through “genetic pollution” (Parker *et al.* 1999).

There has been little mention in the literature of the occurrence of hybridization between indigenous and invading crayfish, e.g. *A. astacus* and *A. leptodactylus* (Cukerzis 1968), although in that case both belonged to the same genus and were of European origin. Unique genetic documentation has been provided by Perry *et al.* (2001, 2002) for hybridization between indigenous and invading *Orconectes* species. Using diagnostic nuclear and mitochondrial DNA markers, along with morphological data, these authors compared crayfish from allopatric and sympatric populations of the invasive *O. rusticus* and of the indigenous *Orconectes propinquus* (Girard) and *O. virilis* (Hagen) in Wisconsin. Hybridization occurred between *O. rusticus* and *O. propinquus* in sympatric sites, whereas *O. virilis* hybridized with neither of these species. A detailed study of the dynamics of hybridization conducted in Trout Lake showed that over 6% of the crayfish were F₁ hybrids, 4% were F₂ individuals (hybrids of hybrid origin), and 13% were backcrosses (product of hybrid × parental genotypes). The majority of F₁ hybrids (95%) were the result of *O. rusticus* females mating with *O. propinquus* males; only 1% of the total crayfish population was the product of F₁ hybrids backcrossing to *O. propinquus*, whereas 13% represented backcrosses to *O. rusticus*. The F₁ hybrids, therefore, appeared to mate disproportionately with pure *O. rusticus* that led to much greater genetic introgression of nuclear DNA from *O. propinquus* to *O. rusticus* than in the reverse direction. A consequence of this is the gradual elimination of *O. propinquus* genes from the population.

among crayfish species (Ferry *et al.* 2002). The implication of Ferry (2002) study is clear that hybridization and introgression pose a substantial threat to the conservation of crayfish biodiversity and that further research is required to test the potential for hybridization among resident and introduced species. These studies have the potential to predict species at risk of losing their genetic identity.

Effects on communities

While NICS clearly cause direct impacts on prey or on competitors and change their abundance and distribution, they may also indirectly change interactions within communities that sometimes result in trophic cascades.

A large variety of articles has shown that, because of their omnivorous nature, introduced crayfish can profoundly modify the trophic structure of freshwater communities at several levels, often acting as keystone species (*sensu* Paine 1966). They also display a wide plasticity in their feeding behaviour, switching from detritivore/scavenger to herbivore/carnivore habits in response to food availability (Hobbs *et al.* 1989). For instance, the large niche breadth and trophic diversity shown in the gut contents of a naturalized *P. clarkii* population in Portugal denoted that a wide variety of aquatic macroinvertebrates is consumed by this species and that the specific composition of the diet changes according to its seasonal availability (Correia 2002).

Several experimental studies, most often conducted in the littoral zone of lentic systems (an exception in Stenroth and Nyström 2003), have demonstrated the direct and indirect trophic effects that NICS have on the food web structure. On the contrary, little is known about the influence directly or indirectly exerted by NICS on e.g. the pelagic compartments of the invaded systems. Figure 4 attempts to summarize the trophic links that NICS may produce in littoral zones of ponds and lakes (see also Nyström 1999, 2002). All these effects are often density dependent (e.g. Charlebois and Lamberti 1996) even if relatively low densities of the potentially invasive *O. virilis* (Chambers *et al.* 1990), the invasive *O. rusticus* (e.g. Lodge *et al.* 1994) and *P. clarkii* (Gherard and Acquistapace 2007) can dramatically reduce biomass and species richness of submersed macrophytes and the abundance of invertebrate prey. The impact on food web structure may also be influenced by the digestion rate of the crayfish species (e.g. Bernardo and Ilhéu 1994), the species composition of the community (Nyström 2002), and the presence of a second introduced predator (Nyström *et al.* 2001), all conditions that make any generalization provisional.

Young and adult NICS are represented in Fig. 4 as different components of the food web, as supported by the literature (Nyström 1999). In fact, although omnivorous crayfish, at least in the laboratory, can efficiently prey upon juvenile or adult fish, amphibian eggs and tadpoles, and macroinvertebrates (e.g. Gherard

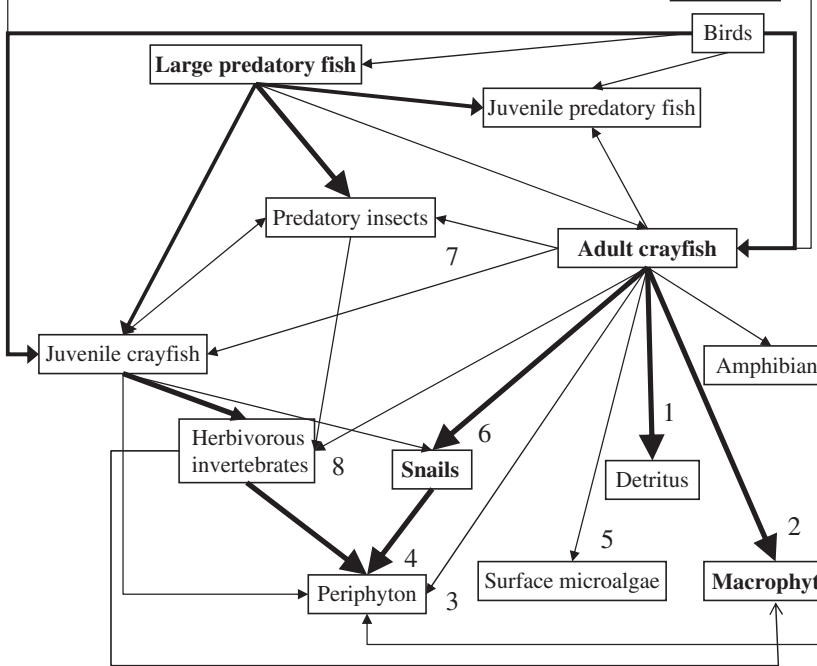


Fig. 4 Food web links (those numbered are discussed in the text) in a littoral zone lake or pond. Arrow thickness denotes the hypothesized strength of the interaction. The most important interactors in the food web are in bold.

2001, Renai and Gherardi 2004) including juvenile crayfish, the guts of several species contain a large proportion of organic detritus and plants, especially macrophytes, whereas juveniles feed predominantly upon macroinvertebrates (Momot *et al.* 1978, Momot 1995). For instance, in a Swedish stream, 40% of the adult *P. leniusculus* were found to have consumed invertebrates as opposed to 87% of the juveniles (Nyström 1999). In a laboratory study, adult *P. leniusculus* even exhibited feeding preference for plant food over animal food when the energetic cost of active predation was high (Ilhéu and Bernardo 1993a, 1993b). When kept together, juveniles may be easily cannibalized by adults. However, the cannibalistic behavior of crayfish has not been confirmed in field studies (Momot 1995), although it is expected to be most severe upon molting in juveniles in the wild (Reynolds and O'Keeffe 2005). The presence of crayfish remains in crayfish stomachs in enclosures was assumed to derive from the cannibalistic consumption of their exuviae (Stenroth and Nyström 2003). Additionally, large predatory invertebrates and fish can reduce the abundance of juvenile crayfish (Nyström 1999). Subsequently, young crayfish have less influence

exerted on them by vertebrate and invertebrate predators.

Typically, adult NICS affect the biomass of organic detritus (link 1, Fig. 4) and biomass of macrophytes (link 2, Fig. 4). In their turn, changes in detritus and macrophyte biomass have multiple non-trophic effects on the community, because of the role of either protective cover or substrate and breeding sites for a multitude of organisms. Detritus is considered to be a highly nutritive food for crayfish through “microbial conditioning” or “chemical-defense leaching” (Newman 1993) for their easier handling by crayfish (Cronin *et al.* 2002). It may be preferred over green plants in laboratory experiments (Ilhéu and Bernardo 1995) and has been often found in gut contents of *P. clarkii* (Ilhéu and Bernardo 1993b, Gutierrez-Yurrita *et al.* 1998) and *P. leniusculus* (Stenroth and Nyström 2003).

The intense grazing on aquatic macrophytes by *O. rusticus*, *P. leniusculus*, and *P. clarkii* (e.g. Lodge *et al.* 1994, Nyström *et al.* 1996, Gherardi and Acquistapace 2007), coupled with their non-consumptive plant clipping and uprooting (Lodge *et al.* 1994, Nyström and Strand 1996, Smart *et al.* 1996, Gherardi and Acquistapace 2007) and their preference for seedlings rather than for older plants (Nyström and Strand 1996), may induce a significant decrease in macrophyte abundance. In enclosure/exclosure experiments, *O. rusticus* at a density of 19 g m⁻² reduced total macrophyte biomass of 64%, while abundance >140 g m⁻² eliminated all macrophytes in 12 weeks (Lodge and Lorman 1987). More than 80% of macrophyte biomass was lost about 20 years after *P. clarkii*'s introduction in the Doñana National Park (Spain) (Gutiérrez-Yurrita *et al.* 1998). The destruction of much more plant tissue than the crayfish consume (Lodge 1991) may induce a positive effect to the system, because fragments could produce nutritious coarse particulate organic matter (CPOM) (Vanni *et al.* 1980). However, macrophyte destruction in nutrient-rich conditions, particularly in eutrophic shallow lakes, is generally followed by a switch from a clear to a turbid state dominated by surface microalgae, like *Microcystis* growth (Rodríguez *et al.* 2003). In its turn, this may lead to a decrease in primary production of macrophytes and periphyton due to the reduced light penetration.

By feeding selectively (Lodge and Lorman 1987, Nyström *et al.* 1996), *P. clarkii* may reduce the biodiversity of macrophytes and even control aquatic weeds (Warner and Green 1995). Cronin *et al.* (2002) studied feeding preferences of *P. clarkii* among 14 species of freshwater macrophytes (including macroscopic algae) and measured this species' response to manipulating the combined plant traits of morphology, toughness, and surface features. Their response to chemistry. The preference of crayfish was related to the presence of phenolics, protein, nitrogen, fiber, lignin, cellulose, ash, and carbon. Like generalist herbivores or omnivores (reviewed in Cirujano *et al.* 2004, Anaños *et al.* 2005a), *P. clarkii* seems to base its feeding decisions on multiple plant traits, such as morphology, structure, chemical defenses, and nutritive value. Often, it feeds upon plants whose finely branched or filamentous morphology

dional value. Similarly, *O. rusticus* consumes single-stemmed species more readily than branched forms (Lodge and Lorman 1987). NICS usually avoid plants, which are chemically defended by multiple compounds, notwithstanding their high concentrations of protein, nitrogen, and dry mass (Lodge *et al.* 1998). The preference for some macrophyte species (e.g. *Chara* L. Linnaeus vs. *Ceratophyllum submersum* Linnaeus) can even influence *P. clarkii* distribution and abundance, as found in a Spanish wetland (Cirujano *et al.* 2004).

However, no single macrophyte trait appears to be a good predictor of macrophyte palatability and factors other than plant tissue quality and morphology, such as plant cover or protection from predators afforded by the plant (e.g. Damman 1991), the consumer's state or hunger (e.g. Cronin and Hay 1996), and the consumer's prior feeding experiences (e.g. Dorn *et al.* 2001), may also be important in determining feeding decisions. Differences in the impact of crayfish on macrophyte growth were also found to be related to crayfish sex and activity, and to the abundance of alternative foods (Chambers *et al.* 1990).

NICS may affect periphytic algae (link 3, Fig. 4) in a number of ways that may result in positive (+) or negative (–) effects by: (1) consuming and displacing periphyton during feeding, movement, or burrowing (–), (2) reducing the abundance of algivorous invertebrates (or vertebrates), which can indirectly increase algal abundance (+) (Luttenton *et al.* 1998); (3) fertilizing periphyton with their faeces (+) (Charlebois and Lamberti 1996); and (4) consuming and destroying macrophytes on which some algae grow (–) (Lodge *et al.* 1994). Therefore, periphyton responses to the crayfish impact are expected to vary as a function of the effect that prevails in the system. Due to the morphology of the feeding apparatus, *O. rusticus* and *P. leniusculus* are not as efficient grazers of microalgae as snails are (Lodge *et al.* 1994, Luttenton *et al.* 1998, Nyström 1999, Nyström *et al.* 2001) and their consumption is not so intense as to outweigh the positive indirect effect of the crayfish-induced reduction in snail densities (the crayfish–snail–periphyton link is strong). Other potential periphyton grazers, e.g. amphibian tadpoles (Nyström 1999) and herbivorous insects, may be preyed on by crayfish but probably their consumption is not so extensive as to produce an indirect positive effect on microalgal abundance (the crayfish–amphibian–periphyton and the crayfish–insect grazers–periphyton links are weak; Lodge *et al.* 1994, Nyström *et al.* 1999). As a result, because snails are both the prey group primarily affected by crayfish and the functionally important grazer group among the many other grazing taxa, crayfish may indirectly generate an increased abundance of microalgae by relaxing the pressure from the grazing pressure of snails (link 4, Fig. 4), thus inducing – although snails being omnivorous – a trophic cascade in the food webs of the littoral zone of lakes or ponds. However, in the habitats characterized by abundant filamentous algae, the intense grazing from crayfish seems not to be sufficient to compensate for the reduced grazing from snails (Nyström *et al.* 1996).

composition of surface (but not pelagic) microalgae (link 5, Fig. 4) has recently found in an *in situ* experiment conducted in a Mediterranean wetland (Gherardi and Lazzara 2006). Six areas (10×7 m) were delimited along a channel in the "Padule di Fucecchio" (Italy) to host crayfish populations at either low (1 m^{-2}) or high (14 m^{-2}) density. The analysis of chlorophyll *a* and *c*, and phaeopigments showed that biomass of surface microalgae, mostly composed of Cyanobacteria, was strongly affected by the presence of dense populations of *P. clarkii*. The potential of their direct consumption by *P. clarkii* was confirmed by behavioral studies that showed crayfish on macrophyte mats feeding on the floating film.

In both lentic and lotic systems, crayfish can have direct and indirect effects on the biomass and species richness of macroinvertebrates (links 6, 7, 8, Fig. 4) as the result of several mechanisms (Charlebois and Lamberti 1993), i.e.: (1) consumption; (2) increased drift through prey escape and incidental dislodgment by their foraging; and (3) possible inhibition of invertebrate reproduction. Each of these mechanisms could have different consequences (e.g., increased mortality vs. displacement to downstream areas) for the local macroinvertebrate assemblage. When crayfish become abundant in lentic systems, species composition of invertebrates may change towards less vulnerable prey species.

Gastropoda are the taxon most affected by NICS (link 6, Fig. 4) and are sometimes eliminated. In Trout Lake, Wisconsin, snails declined from >100 to <5 individuals m^{-2} after 19 years of colonization by *O. rusticus* (Wilson 2004). Also bivalves may be affected by NICS; for instance, predation by *O. rusticus* may have a significant impact on the colonization rate of zebra mussels (Perry *et al.* 1997, 2000).

NICS are selective in their choice of snails, thin-shelled snails being preferred to thick-shelled species because they are easier to handle (Nyström and Nilsson 1998). Hence, in systems invaded by NICS, snail species composition may be altered from the thin-shelled *Lymnaea* spp. to the thick-shelled *Bithynia* spp. (Nyström *et al.* 2001). Large snails are also less profitable, because handling time of shells increases exponentially: adult *P. leniusculus* took less than 1 minute to feed upon small *Lymnaea stagnalis* (Linnaeus) but spent more than 27 minutes handling and consuming large snails. However, in complex habitats such as macrophyte beds crayfish may be less indiscriminate in their selection (Nyström and Pérez 1998). Also crayfish naïveté to a mollusk, though never definitively proved, may influence consumption. In a laboratory experiment Correia *et al.* (2005) showed that *P. clarkii* is able to capture the exotic snail *Physa acuta* (Draparnaud), but never preyed upon the Asian clam *Corbicula fluminea* (Muller). Possibly, prior experience coupled with the availability of alternative prey may be decisive as to whether the predator proceeds with or aborts an attack.

The direct impact of NICS on non-snail macroinvertebrates (links 7 and 8, Fig. 4) largely depends on the life style and behavior of any single species.

enough to escape tactic-feeding crayfish (e.g. isopods, amphipods, Diptera, Heteroptera, and Coleoptera); (2) circumvent crayfish recognition by living in cases (e.g. Trichoptera); or (3) avoid contact by living in the sediment (e.g. some Diptera) (Lodge *et al.* 1994, Nyström *et al.* 1999). In streams, crayfish may have less predictable effects on invertebrate communities than in lentic waters (Stenroth and Nyström 2003) even if, also in lotic systems, slow-moving species are expected to decline (i.e. leeches, dragonflies, caddisflies, isopods, and mollusks) whereas more mobile prey or prey living in sediments seem to be less affected (i.e. chironomids and stoneflies).

The indirect impact of NICS on zoobenthic communities is particularly complex. Through consumption and destruction of macrophytes, crayfish can destroy littoral habitats, leading to declines in macrophyte-associated taxa (Nyström *et al.* 1996). Crayfish may also influence detrital substrates through bioturbation and feeding; the reduction in detritus has potential consequences for zoobenthic communities, particularly collector-gatherers (e.g. some Ephemeroptera, Trichoptera, and Diptera). Finally, crayfish predation upon, or competition with other zoobenthic predators such as Odonata larvae could reduce the occurrence, subsequently leading to an increase in the abundance of their prey (McCarthy *et al.* 2006).

Recently, the effects of *O. rusticus* – and of other NICS – on benthic invertebrate densities were examined by McCarthy *et al.* (2006) by applying an effect model meta-analysis on pre-existing data. A comparison was made between cage experiments conducted in 14 studies that excluded crayfish as the control and maintained a given density of crayfish as the treatment. The negative effect of crayfish on the total invertebrate abundance appeared to be driven by the significant decline of a few taxonomic orders, specifically Gastropoda and Diptera (Fig. 5). However, the abundance of Amphipoda, Coleoptera, Ephemeroptera, Oligochaeta, and Trichoptera was also reduced in crayfish treatments, although results for these taxa were not significant. Comparisons across studies showed that the greatest negative impact was exerted on Gastropoda (followed by Diptera, Amphipoda, and Ephemeroptera).

Finally, NICS can be prey items for fish, birds, and mammals, constituting a new resource for higher trophic levels in several areas of their introduction. In the Lower Guadalquivir Basin (Spain), before the introduction of *P. clarkii*, eels mostly preyed upon fish species (mosquitofish and carp). After crayfish introduction, only 17% of their stomachs (vs. 50% before crayfish introduction) contained other fish species, whereas the dominant prey item was *P. clarkii*, reaching 67% of occurrence (Montes *et al.* 1993). As they readily feed on *P. clarkii*, eels were proposed as selective biological control organisms (Montes and Frutiger 2001). Still in southern Spain, *P. clarkii* is also an important part of the diet of at least six bird species, in particular white storks, great herons, and little egrets, whose diet is composed of up to 80% of crayfish (Rodríguez *et al.* 2005). Though no quantitative study has been yet

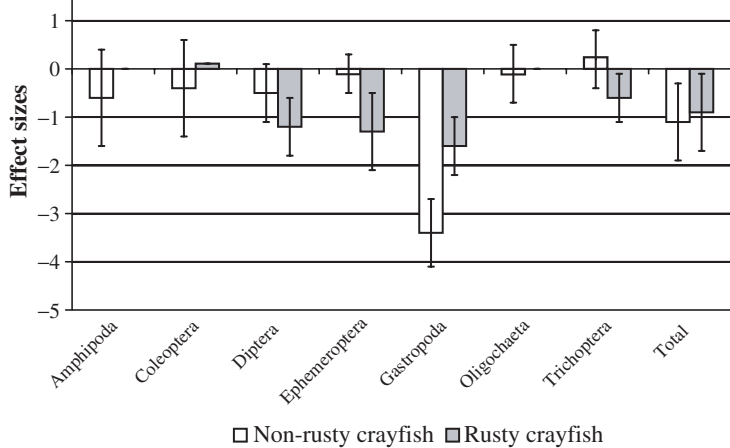


Fig. 5 Results from a fixed-effect model meta-analysis applied by McCarthy *et al.* on data obtained from 14 enclosure/exclosure experiments from the published literature. The effect size is the difference between the effects of crayfish on zoobenthic abundance at normal versus elevated densities, measured in units of standard deviation. Effect sizes ($\pm 95\%$ Confidence Interval) are shown for total invertebrate and individual orders. Negative values indicate a negative effect of crayfish on invertebrate density.

the appearance of *P. clarkii* has been considered responsible for the increase in the number of avian species, like some Ardeidae, together with cormorants in some European areas, such as in Massaciuccoli Lake (Tuscany) (Barbarelli and Gherardi 2000). In Doñana National Park it has also become the most common prey category of the otter, *Lutra lutra* (Linnaeus) (Delibes and Adrian 1994).

Notwithstanding the large amount of available data, much information still derives from short-term studies and therefore the long-lasting strength of the link can only be hypothesized. A few long-term studies have attempted to analyze – all the other factors being equal – changes in species richness after the introduction of NICS. The study of Rodríguez *et al.* (2005) reviewed existing information on the communities before the appearance of *P. clarkii* in Chozas Lake (Spain) and compared it with the data collected after its invasion. For macroinvertebrates, data from proximal non-invaded wetlands were used in the analysis. The results (Table 1) were clear in showing the decline of submerged vegetation and the decrease of macroinvertebrate populations, leading to a dramatic depletion of food resources, shelters, and breeding sites for fish, amphibians, and birds.

In a northern temperate lake in Wisconsin, USA (Sparkling Lake), McCarthy *et al.* (2006) conducted a 24-year time series analysis of *O. rusticus* and other zoobenthos abundances. As a confirmation of a companion study (see also

	Before	After	Lo
Vegetation cover (%)	95	<3	
Macroinvertebrates (genera, number)	31	9	
Waterfowl (species, number)	50	26	
Amphibians (species, number)	6	1	

this crayfish species was found to exert a significant, although variable, impact on zoobenthic communities, its abundance being negatively correlated with the abundance of total zoobenthos and of Diptera, Ephemeroptera, Odonata, Trichoptera. However, the authors proved that the invertebrate taxa had a high resilience in the long term. Nearly all invertebrate taxa were negatively affected by the crayfish within a 1-year lag, but no taxa exhibited sustained decline over the course of the *O. rusticus* invasion. Several factors may explain this pattern. Large-bodied invertebrate taxa, such as snails and crayfish, have slow generation times and are not as productive as smaller taxa, and are thus unable to respond numerically following population reductions of crayfish. In addition, aquatic insect larvae have a winged adult stage and, as a consequence, a great dispersal ability – thus facilitating quick recovery. Whatever the explanation might be, McCarthy *et al.*'s (2006) results are illustrative in underlining the importance of a long-term monitoring of the invaded community to capture the complex picture of the impact of NICS.

Effects on ecosystems

As compared with the individual, population, and community levels, documented changes to ecosystem processes have been rarely reported in the literature on NICS. This probably reflects a lack of measurements of ecosystem processes rather than a lack of impact on these processes. The abundantly documented community effects are on the contrary expected to determine significant changes in energy flux and nutrient cycling in the invaded systems.

Essentially, the introduction of NICS may alter the pathways of the energy flux in two ways, i.e. through augmenting connectance by feeding at several trophic levels and through increasing the availability of autochthonous resources as a food source for higher trophic levels (Stenroth and Nyström 2003). This was clearly proved by Geiger *et al.* (2005) in temporary freshwater marshes in Spain. Before the introduction of *P. clarkii* (Fig. 6a), macrophytes and associated periphyton were the dominant primary producers. Only a small portion of the energy was transmitted from them to herbivores, whereas most

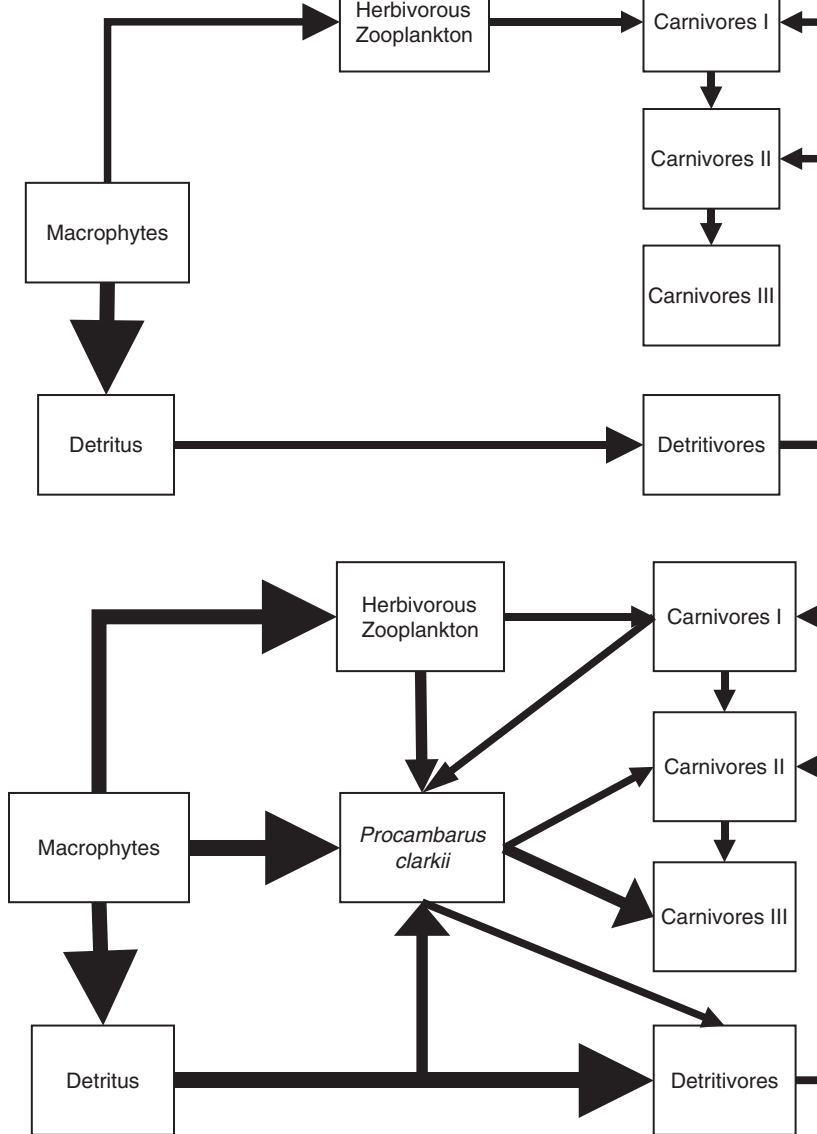


Fig. 6 Hypothesized energy flows in a marshland system before (A) and after introduction of an NICS (*Procamburus clarkii*). (Modified after Geiger *et al.* 2005)

it was lost to the detritus pool, which accumulated large amounts of organic matter. Detritivores, mainly macroinvertebrates (oligochaetes, chironomids, and meiofauna (nematodes, ostracods), used only a small fraction of

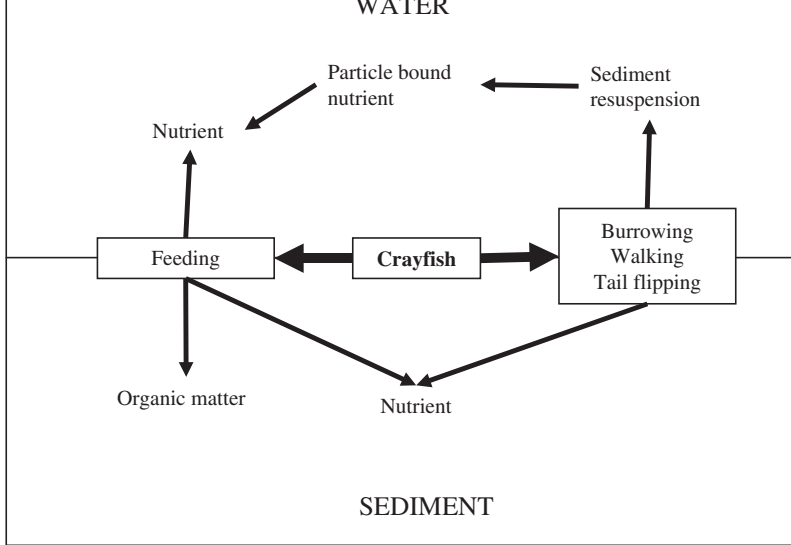


Fig. 7 Effects of the benthic activity of an NICS (*Procambarus clarkii*) on physicochemical characteristics of water and sediments in a floodplain wetland in Spain (Modified after Angeler *et al.* 2001)

deposited material. This system was characterized by a high diversity of invertebrates and consisted of a minimum of four levels of consumers. Due to the large number of trophic levels and losses of energy to the detritus pool, the energy transferred to top predators such as birds and mammals was comparatively low. After the introduction of crayfish (Fig. 6B), much of the detritus was consumed by *P. clarkii* and the energy gained was directly transferred to the top predator level (fish, birds, and mammals). This resulted in a decreased importance of macrophytes, herbivores, and primary carnivores but offered a larger availability of energy for vertebrate predators.

The role that NICS may play through their benthic activity on physicochemical characteristics of water and sediments was investigated by Angeler *et al.* (2001) in a floodplain wetland in Spain. *Procambarus clarkii* was hypothesized to affect the ecosystem processes by: (1) recycling sediment bound nutrients and (2) resuspending sediments associated with crayfish foraging, burrowing, and locomotory activity (walking, tail flipping) (Fig. 7). Compared to the control, the enclosures with crayfish showed a significant increase in dissolved inorganic nutrients (soluble reactive phosphorus and ammonia) and total suspended solids as a result of crayfish bioturbation. At the same time, crayfish reduced the content of organic matter in the sediment and sludge.

benthic activity.

Crayfish-mediated bioturbation has the general effect of impoverishing water quality by increasing total suspended solids and hence turbidity and reducing light penetration and plant productivity (Anastácio and Ma 1997, Rodríguez *et al.* 2003). Crayfish may also alter sediment characteristics as a result of oxygen supply due to their activity. Bioturbation is often associated with crayfish constructing burrows, as commonly observed in *P. clarkii*, *P. leniusculus*, and *C. destructor* (e.g. Sommer and Goldman 1983, Gutierrez Yurrita and Montes 1999). However, crayfish, like *O. limosus*, can also disturb bottom sediments due to the friction between the extremities of its pereopods and the bottom during walking, the force exerted above the bottom by the uropods and the telson of escaping crayfish, and the pressure of the uropods and claws into the substrate to slow its movement while walking in fast currents (Maude and Williams 1983). In experimental flumes, Statzner *et al.* (2003) showed that *O. limosus* at a fixed biomass (174 g m^{-2}) significantly affected sand and gravel erosion. Its effect of bioturbator varied in function of the presence of refugia and aggression: sediment erosion averaged $2.1 \pm 1.4 \text{ kg dry weight m}^{-2} \text{ d}^{-1}$ when crayfish hierarchies were established and refugia were available. Once the refugia were removed, these rates increased to 4.0 and $3.2 \text{ kg dry weight m}^{-2} \text{ d}^{-1}$. Additionally, bioturbation by crayfish was found to change bedform roughness, physical particle consolidation, proportion of sand in gravel interstices, sand cover by gravel, and the cover of filamentous algae. Such changes, in turn, may affect the abundance and structure of the entire benthic community, e.g. by modifying their substrate or by reducing algae and biofilm available for grazers. Also, sand reduction among gravelers might alter the egg survival of gravel-breeding fish, like salmonids.

WHY DO NICS CAUSE MORE PROBLEMS THAN INDIGENOUS CRAYFISH?

In areas without any indigenous ecological equivalent, the changes caused by the introduction of NICS may be complex and usually affect all levels of ecological organization. Impacts range from subtle behavioral modifications of resident species to altered energy and nutrient fluxes in the ecosystem. Impacts at the community level can be strong when the introduced crayfish experience little predation or competition from native predators and have prey that lack efficient defense adaptations to them (Nyström *et al.* 2001). The mode of resource acquisition by NICS and their capacity to develop new trophic relationships, coupled with their action as bioturbator, may lead to dramatic direct and indirect effects on the ecosystem.

When NICS replace an indigenous ecological equivalent, their resource acquisition mode should not be novel to the colonized community and the

strongly, once introduced, they are capable of building high densities and reaching large size. Indeed, several introduced crayfish often reach much higher densities than indigenous crayfish, e.g. *P. leniusculus* vs. *A. pallipes* (Gua Wiles 1996). Densities of *O. limosus* ranged between 0.4 and 77 m⁻² in a reservoir in Poland, of *O. rusticus* between 0.18 and 21 m⁻² in North American streams, and of *P. leniusculus* between 3.7 and 21.7 m⁻² in an English stream (reviewed in Nyström 1999). On the contrary, densities of the indigenous species have been estimated to reach a maximum of 14.3 m⁻² for *A. astacus* (in a Swedish lake), 3 m⁻² for *A. pallipes* (in France), 3.6 m⁻² for *C. japonicus* (in Japan), 0.83 m⁻² for *P. fortis* (in USA), and 3.3 m⁻² for *Paraneopantodon planifrons* White (in New Zealand) (references in Nyström 1999). The decline of biota recorded by Wilson *et al.* (2004) in Trout Lake, Wisconsin (USA), when *O. rusticus* catches reached a threshold of nine crayfish trawls suggests that its high abundance is the primary reason for its large impact on biota in lakes with pre-existing crayfish populations.

Several biological traits contribute to the achievement by crayfish of high densities/large size. Relatively to indigenous crayfish, some NICS are characterized by higher fecundity, faster growth rates, and better physiological tolerance to changing environmental conditions (Lindqvist and Huner 1999, Chilton 2002, 12). They also might be better at coping with changes induced by human activities that cause pollution and habitat destruction. For instance, *P. leniusculus* is a good colonizer of disturbed aquatic habitats and can survive in adverse conditions in burrows (Gherardi 2006). Also, higher survival rate, leading to higher densities and/or larger sizes, is expected when a species is introduced without a full complement of specific parasites, pathogens, and natural enemies. And large sizes, in their turn, make crayfish both resistant to size limited predators (such as many fish) and agonistically superior in resource competition and fights. As a consequence, because of their large numbers, coupled with wide trophic plasticity, NICS exert a greater direct (through consumption) or indirect (through competition) effect on the other biota, particularly on indigenous crayfish species, benthic fish, mollusks, and macrophytes (Nyström 1996). This is also true for those species that apparently have not caused much environmental degradation, such as *A. leptodactylus* in England, whose high numbers are producing considerable problems for anglers (Hart 1999b). Obviously, large size usually translates into an overall higher energy and nutrient demand, but NICS may also be more efficient energy converters and may display higher metabolic rate when compared with similarly sized indigenous crayfish species.

As a consequence, a combination of larger size and greater weight-specific consumption of macrophytes and snails may explain the greater ecological impact suffered by those North American lakes where *O. rusticus* had replaced its congeners (Olsen *et al.* 1991) (Table 2), whereas the more efficient growth of *P. leniusculus* than *A. astacus* seems to be the cause of the dramatic decline

the greater impact of *Stenotres rubatus* (Or) relative to *S. propinquus* (Op) and *S. hiemalis* (Ov) on a benthic community structure.

Mechanisms	Replace Op	Repl
1. Individual size	Or > Op	O
2. Population density	Or < Op	O
3. Population biomass	Or < Op	O
4. Weight-specific consumption, C, and sublethal damage, D, of snails	C: Or > Op D: Or = Op	C: O D: O
5. Weight-specific selection for single-stemmed macrophytes	Or = Op	C
6. Weight-specific consumption, C, and destruction, D, of macrophytes	C: Or > Op D: Or = Op	C: C D: C

of macrophytes biomass (including the extinction of several rare *Chara* spp.) as recorded by Nyström and Strand (1996) in Sweden.

EFFECTS ON HUMAN ECONOMY AND HEALTH

From an anthropocentric perspective, a useful approach to measure impact is to assess the damage caused by NICS by calculating the economic costs induced to human societies, also in terms of the social and ethical problems associated with their potential harm to human health. A review of the existing literature in the matter shows that much of the discussion has been purely anecdotal. A negative consequence is the often encountered difficulty in conveying to decision makers the need of containing the spread of NICS and mitigating the risks they pose.

The introduction of NICS has been often assumed to have contributed in a positive way to human economy by: (1) restoring some traditions promoting the cultural heritage of a country, e.g. crayfishing in Sweden and Finland (Kirjavainen and Sipponen 2004); (2) producing some economic benefits for many families in poorly developed areas, e.g. in Andalusia, Spain (Geiger 2005); (3) leading to a diversification of agriculture to include astaciculture by crayfish farmers in Britain and in Spain (Holdich 1999a); and (4) increasing trade between countries inside Europe as well as between European and non-European countries (Ackefors 1999).

There are, however, several examples showing that often the introduction of commercially valuable crayfish has also led to negative results in the marketplace. Despite the original aim of crayfish farmers in Britain to produce crayfish for export to the Scandinavian market where they fetch a high price (Holdich 1993), most of the exports are now being made with crayfish harvested

few of the several projects that led to crayfish importations since the 1970s can be regarded as successful (de Moor 2002). For instance, in Lake Naivasha, Kenya, only about 40 metric tons of *P. clarkii* are now caught annually and exclusively for local consumption (mainly tourism), after their first harvest in 1975 of several hundred tons per year (Smart *et al.* 2002). Crayfish are now reported to spoil valuable fish (tilapia and largemouth bass) caught in gillnets (up to 30% of the catch) and to damage fish nets (de Moor 2002). They are also responsible for the decline of the rooted vegetation and therefore of the increase of phytoplankton, decrease of water transparency, and reduction of fish, including commercial species, in the littoral zone (de Moor 2002).

In several countries, introduced crayfish have today much lower commercial values than indigenous species, as exemplified by the Scandinavian market where consumers are willing to pay substantially higher prices for the indigenous *A. astacus* than for the naturalized *P. leniusculus* (Holdich 1999a). Crayfish farming, in its turn, may produce extensive environmental impacts and associated costs, as the result of the continuous roaming of fishermen, causing a physical alteration of the habitat and the capture of non-target organisms (e.g. turtles) in the crayfish traps (Geiger *et al.* 2005).

There are several examples of damage to other human activities. *Procambarus clarkii* is a recognized pest in rice cultures in various parts of the world. Although in Louisiana (USA) double cropping crayfish and rice are practiced with success (Chien and Avault 1980), the species produces economic losses in rice fields in Portugal (Correia 1993). As an example, economic losses per hectare of Euro 43.40 of the 2004 rice production (a 6.3% decrease in profits) were reported in the “Baixo Mondego” area exclusively due to crayfish (Anastácio *et al.* 2005a). Damage to rice production primarily consists of crayfish consuming seedlings, but negative effects derive from the increased turbidity, decreased dissolved oxygen content due to the crayfish bioturbation (Anastácio *et al.* 2005a, b, c).

Burrowing by several NICS (e.g. *P. clarkii*, *P. leniusculus*, and *C. destructor*) can be a problem in areas other than agricultural, e.g. lawns, golf courses, lawns, dams, dykes, and in rivers and lakes (e.g. Anastácio and Marques 1997). Several authors have lamented the damage caused by *C. destructor* burrowing to concrete walls and irrigation canals (de Moor 2002). More often cited is the damage of *P. clarkii* to “honeycomb” banks, with their consequent structural damage (Huner 1977) that seriously affects areas with extensive canal irrigation systems and water control structures (Adão and Marques 1993). Although not recorded as a burrowing species in its native North American habitat (Holdich 1999a), *P. leniusculus* causes considerable damage to river banks by burrowing in the UK (Sibley 2000).

Indeed, if a monetary value were to be assigned to species extinction, the losses in biodiversity, ecosystem services, and aesthetics, the total economic damage of introduced crayfish might be enormous. Neither do we have re-

US\$4.5 million for the resuscitation of *P. fortis* in California (USFWS 1997, US Fish and Wildlife Service) and the £100,000 spent trying, unsuccessfully, to eradicate *P. leniusculus* from rivers in Scotland (Collins 2006).

Up to today, little attention has been paid to the potential harm that NICS may pose to human health. NICS, such as *P. clarkii*, often live in areas contaminated by sewage and toxic industrial residues and may have high heavy metal concentrations in their tissues (Geiger *et al.* 2005); they were found to bioaccumulate metals such as nickel, lead, and zinc in their tissues and organs at a significantly higher rate than the indigenous species (Gherardi *et al.* 2006). Their potential to transfer contaminants to their consumers, including man, is obviously high. Measurements of accumulation of heavy metals in waterbirds and other wetland birds living and feeding in a toxic spill area of Spain showed that heavy metals like arsenic have entered the food chain and were detected in some bird species, such as white storks, spoonbills and grey herons, all prey of crayfish (Geiger *et al.* 2005).

The finding that *P. clarkii* may consume Cyanobacteria is of increasing concern for human health (Gherardi and Lazzara 2006). Several Cyanobacteria release a wide range of toxins and BMAA (β -N-methylamino-L-alanine) which may produce lethal animal and human intoxications (e.g. Carmichael 1989, Cox *et al.* 2005). Among the few organisms so far investigated, *P. leniusculus* and *P. clarkii* were found to accumulate such toxins in their tissues (Lirio *et al.* 1998, Vasconcelos *et al.* 2001), being therefore able to transfer them to their sensitive organisms, man included.

The other side of the coin is the ability of *P. clarkii* to control, through predation and competition, populations of the pulmonate snails *Biomphalaria* and *Bulinus* known to host *Schistosoma mansoni* and *S. haematobium*, the cause of human schistosomiasis (Chapter 4). Schistosomiasis is one of the most widespread diseases in Africa: in Kenya alone, it is known to affect 3.5 million individuals with 12 million more at risk of infection. As suggested by Mkoari (1999), due to the quick spread of this crayfish in African waterbodies, the epidemiology of schistosomiasis is expected to be significantly altered with time, although the possibilities remain that African snails will soon evolve mechanisms to avoid crayfish predation before their extinction or that the parasite will change its host.

WHAT COMES NEXT?

Despite the considerable attention that NICS have received since 1987, a number of the many papers published in the last few years has revealed the absence of a literature of a general framework about their impact. Nonetheless, a global approach is required to help us coordinate and improve both control and research for the existing NICS and hopefully predict the impact of future introductions.

the impact of NICS at multiple ecological levels. This is unfortunate, because to fully understand the range of the impact observed (Simon and Town 2003). Also, little effort has been made to study the impact of NICS at the genetic level. We cannot even guess therefore what their role might be in determining the future evolutionary pathway that the invaded system will follow after the introduction of NICS. Neither do we have quantitative estimates about direct or indirect monetary (and social) costs induced by NICS on the human economy and health. And only a few paradigmatic invasive species, namely *P. leniusculus*, *P. clarkii*, and *O. rusticus*, have been extensively studied, whereas information is scanty or even absent about other species such as *C. destructor*.

Short-term laboratory and field studies have revealed a myriad of direct and indirect effects of crayfish on some compartments of the invaded ecosystem (most often the littoral zone). Their results were certainly able to provide mechanistic insights into the interactions between crayfish and the other organisms in the community and to quantify the immediate impact of the invader. However, these sometimes complex interactions have been only seldom investigated at larger levels. Few comparative field studies (e.g. Charlebois and Lamberti 1996) and even fewer long-term studies (Wilson *et al.* 2004, McCarthy *et al.* 2006) have been conducted to examine the dynamic relationships among organisms, including the prolonged effects of crayfish invasion on native communities over multiple generations.

Indeed, coupling the results of small- and large-scale studies may help construct a more realistic picture of the impact of NICS. As held by McCarthy *et al.* (2006), each method is not without its own biases. Along with characterizing short-term ecological responses, small-level studies may suffer from experimental artifacts. In contrast, long-term studies certainly provide important insights into the long-term threats of an NICS and the potential adaptability of the native taxa to it, but their results may also be confounded by environmental factors that cannot be controlled (Parker *et al.* 1999). Because the disadvantage of one approach is the advantage of another, coupling multiple levels of analysis certainly provides a method in which interactions at one level can be successfully translated to another.

Finally, we need much more intensive work on the whole-system impact of the crayfish invasion; specifically, we need to learn more about the natural variability among systems and the extent to which the impact of an NICS depends on the community or ecosystem where it is measured. So, on what level can we generalize across systems? And how often does the impact of a crayfish invasion depend on the presence of other NIS? Not before having answered to these questions, to the other questions above will we be able to generalize, and even predict which species is more likely to have the greatest impact in aquatic systems (Parker *et al.* 1999).

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